

chapter 31

Competition and Community Organization on Hard Surfaces in the Sea

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INTRODUCTION

Investigations of interspecific competition in the sea have flourished at many levels in the past decade. Significant progress has been made in demonstrating that competition chronically occurs on a wide variety of marine hard grounds (Jackson 1977a, 1983); in determining the relative interference competitive abilities of co-occurring species (Lang 1973; Stebbing 1973; Jackson and Buss 1975; Osman 1977; Buss 1979a, 1980, 1981a, 1981b; Buss and Jackson 1979; Jackson 1979b; Karlson 1980; Keen and Neill 1980; Grosberg 1981; Kay and Keough 1981; Rubin 1982; Russ 1982; Sebens 1982; Ayling 1983; Paine 1984); in correlating competitive success (or failure) with environmental conditions or traits of particular organisms (Connell 1961a; Day 1977; Jackson 1979b; Buss 1979b, 1980, 1981a, 1981b; Osman and Haughness 1981; Russ 1982; Rubin 1982); in elucidating the mechanisms by which one species overcomes another (Lang 1973; Buss 1979b, 1981b; Buss et al. 1984); and, finally, in documenting that similar competitive interactions occurred

repeatedly throughout the fossil history of groups known to compete actively today (Brasier 1976, Fritz 1977, Stel 1978, Taylor 1979, Lidell and Brett 1982, Lidgard and Jackson 1982).

Coincident with this expanding knowledge of competition on hard surfaces in the sea, the study of predation and physical disturbance has proceeded at a meteoric rate. These studies, particularly in the rocky intertidal zone, have repeatedly demonstrated that predation and disturbance can act to hold the densities of potentially competing species to a level so low that contact-mediated competition between certain structurally or numerically dominant taxa is reduced or even precluded. This suggestion, initially called the predation hypothesis (Paine 1966) and also known, in modified form, as the intermediate disturbance hypothesis (Connell 1978), is based on field experiments repeated several times and in several locations (Paine 1966, 1971, 1974; Paine and Vadas 1969; Harper 1969; Dayton 1971; Menge 1976; Lubchenco 1978, 1980; Lubchenco and Menge 1978; Sousa 1979; and many others).

How might the repeated observations of competition on marine hard substrata be reconciled

with the repeated experimental demonstration that predation acts to reduce or preclude the occurrence of competition? It is the object of this chapter to investigate this dilemma. Hypotheses are sought that specify the conditions under which competition will or will not be observed in ecological time.

The first section of this chapter summarizes a specialized subset of the competitive interactions on marine hard grounds, focusing mainly on competition for space. I discuss the occurrence, costs, and mechanisms of competition; the phenomenon of competitive ranking; the pattern of available space and its renewal; and correlates of competitive success such as colony size, population density, and growth morphology. In the second section I briefly review the predation hypothesis and note its limitations. In particular, settlement rates, prey resistance to predators, limitations on predators, refugia, and prey clonality are some factors that permit competition to persist in the face of the predation. In the last section I present a reconciliation of the predation hypothesis with observations of competition. In each section I do not attempt an exhaustive review or enumeration; rather, I present vignettes of particular empirical investigations, chosen largely from my own work.

Both the origin and the subsequent development of the ideas in this paper lie in my collaboration with Jeremy B. C. Jackson. We have discussed at length all of the issues treated here on numerous occasions over the last ten years. While he is not responsible for any failing of this particular rendering of our collaborative efforts, he most certainly shares any success this attempt at provisional synthesis might enjoy.

ON OBSERVING COMPETITION

Occurrence of Competition

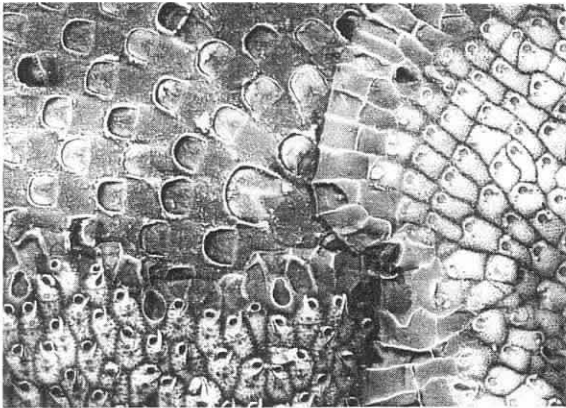
Competition between sessile marine invertebrates occupying marine hard substrata may involve interactions for food, light, and space. The study of competition for light almost always requires direct experimental intervention. One must remove a species to remove presumptive shading effects and document the growth or reproductive success of the other species. A number of such studies

have been performed in rocky intertidal environments, and several have demonstrated competition (see review by Lubchenco and Gaines 1981).

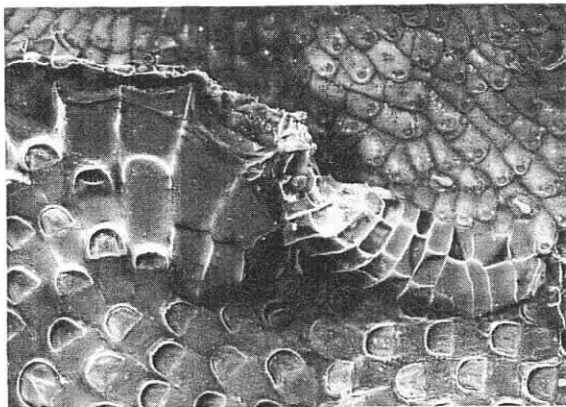
The study of competition for food is far more difficult. Most sessile invertebrates depend on planktonic food resources. The monitoring of resource levels presents imposing technical problems: plankton populations are never static in distribution, the documentation of the distribution and abundance of plankton is highly labor intensive, and the precise dietary requirements of most invertebrates are largely unknown. Further complicating such analysis is the fact that many invertebrates feed in a low Reynolds number flow regime, in which the actual availability of food to the organism depends not only upon the density of the food in the environment, but also on the detailed fluid mechanics of the particular environmental setting. Despite these rather severe limitations, there have been demonstrations of *in situ* depletion of planktonic food resources (Glynn 1973, Buss and Jackson 1981) and laboratory demonstrations of interference competition for food (Buss 1979b). I know of no case, however, in which competition for food has been documented *in situ* among any sessile marine invertebrates.

Competition for space is by far the easiest form of competition to show, especially between colonial invertebrates. When two such species encounter one another, either of two results may occur: (1) the two colonies cease growth along the shared margin or (2) one or both colonies expands into the space occupied by the other. The latter alternative often occurs as physical overgrowth of one colony by another (Figs. 31.1 and 31.2), frequently resulting in the death of the overgrown tissues. Clonal organisms are typically capable of indeterminate growth and can often expand to cover the limits of the available substratum (Jackson 1977a). Since fecundity increases with colony size in an exponential fashion for clonal invertebrates (Jackson 1977a), the reduction in colony size resulting from overgrowth has an unambiguous effect on an important component of colony fitness. Therefore, both the cessation of growth and the occurrence of overgrowth are clearly competitive encounters.

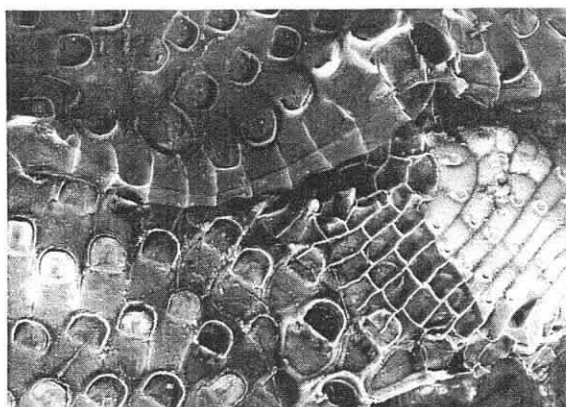
The only exception to the generalization that growth cessation or overgrowth demonstrates the



A



B



C

Fig. 31.1 Examples of overgrowth competition between encrusting bryozoans from Jamaican cryptic coral reefs. (A) *Stylopoma spongities* (right) overgrowing *Repadeonella plagiopora* (lower left) and *Steganoporella* sp. nov. (upper left). Note the giant buds along the growing margin of *S. spongities*. (B) *Stylopoma spongities* (top) overgrowing *Steganoporella* sp. nov. to the right, while *Steganoporella* sp. nov. has raised its growing edge and prevented overgrowth on the left. (C) *Steganoporella* (top) overgrowing *Stylopoma spongities* (middle right) and *S. spongities* overgrowing *Steganoporella* (bottom). The top *Steganoporella* is also overgrowing the bottom colony of *Steganoporella*. (From Jackson 1979b.)



Fig. 31.2 The top of an aluminum beer can collected at 5 m depth near Isla Taboguilla, Panama. Note the almost complete cover by serpulids, barnacles, and bryozoans and the numerous instances of interspecific contact and overgrowth.

existence of competition would be a case in which either (or both) of the two colonies could not survive in the physical environmental regime occupied by the other. The interactive margin would have to lie precisely along a threshold level of some physical environmental factor, such as temperature or flow. Although strong environmental gradients are known to exist in a number of marginal marine environments, such as rocky intertidal shores, these environments are typically dominated by large aclonal organisms (Jackson 1977a, Paine and Suchanek 1983). Clonal groups dominate in the subtidal (Jackson 1977a, 1979b, 1983), where environmental gradients are usually far less pronounced. I know of no evidence for any subtidal species that growth cessation at a colony margin can be attributed to the inability of one organism to persist in the space occupied by the other.

Overgrowth interactions are particularly fruitful for the study of competition. Not only does the observation of overgrowth generally demonstrate that competition occurs, but also the mere inspection of the colonies indicates which individual is dominant in that interaction at that particular time (Fig. 31.1). Overgrowth observations yield only instantaneous data, and any presumption as to the long-term dynamics of an interaction based on such information is necessarily speculative (Stebbing 1973, Buss and Jack-

son 1979). Nevertheless, overgrowth is one of the simplest interactions in which to study competition, and the bulk of the recent data on competition on marine hard grounds is based on these observations.

The occurrence of overgrowth interactions is not limited to Recent environments. Jackson (1983) reviews examples of overgrowth from the fossil record dating back to early in the Paleozoic (Brasier 1976, Fritz 1977, Stel 1977, Taylor 1979, Liddell and Brett 1982, Lidgard and Jackson 1982). Unfortunately, little attempt has been made to quantify these interactions in order to compare them rigorously either to similar interactions within the same stratigraphic unit or to interactions among extant relatives. Such studies, especially in low-diversity communities living symbiotically on gastropod shells, may turn out to have considerable relevance to problems in ecological and evolutionary theory.

Competitive Rankings

Demonstrating that competition occurs is the first level of analysis of competition. The second level is to determine which species wins the encounter. The relative interference competitive abilities of the abundant species within a community are known for several marine communities (Dayton 1971; Lang 1973; Stebbing 1973; Jackson and

Buss 1975; Osman 1977; Buss 1979a, 1980, 1981a, 1981b; Buss and Jackson 1979; Jackson 1979b; Karlson 1980; Keen and Neill 1980; Kay and Keough 1981; Grosberg 1981; Russ 1982; Rubin 1982; Sebens 1982; Ayling 1983; Paine 1984). Rankings of this sort are available for few other communities and play an important role in discussions of community organization in the sea (Jackson and Buss 1975; Connell 1976, 1978; Buss and Jackson 1979; Karlson and Jackson 1981; Karlson and Buss 1984; Yodzis 1978 and Chapter 29; Paine 1984).

Competitive rankings show great variability both between communities and between species within a community. Many such rankings are largely transitive (Lang 1973, Stebbing 1973, Quinn 1982), that is, if A usually beats B and B usually beats C, then A also beats C. However, different results are found in selected subsets of overgrowth rankings from cryptic coral reef communities in Jamaica, cobble communities in England and Panama, piling communities in Australia, and coralline algal pavements in Washington State (Fig. 31.3). In these more diverse systems competitive rankings are far more complex and form networks of competitive relationships that deviate strongly from transitive patterns. The lack of clear transitivity in these instantaneous data is especially intriguing, given the demonstration that intransitive competitive dynamics can give rise to limit cycle behavior in model communities (Gilpin 1975; May and Leonard 1975; Yodzis 1977a, 1978).

The accumulation of data on competitive rankings within communities has led to the identification of the relative competitive abilities of different taxa (reviewed by Jackson 1983). Aclonal organisms are typically dominated by clonal groups, except in physically stressed environments (Greene and Schoener 1982). Among clonal groups, skeletonized organisms (bryozoans, coralline alga, and corals) are typically overgrown by groups that do not deposit a rigid skeleton (demosponges and ascidians). Among skeletonized organisms hermatypic corals, whose symbiotic dinoflagellates enhance the rate at which skeleton is deposited, are typically dominant over aposymbiotic groups. Patterns in relative competitive ability are known within many of these taxa as well. For example, cheilostome

bryozoans with a sheetlike encrusting morphology are typically capable of overgrowing those with a runnerlike encrusting morphology (Buss 1979a, Jackson 1979a). Although clear patterns of this sort have been recognized within and between several taxa in rankings drawn from several communities, the ranking for any community often involves one or more exceptions to these general patterns, leading to cases of highly intransitive within-community competitive rankings.

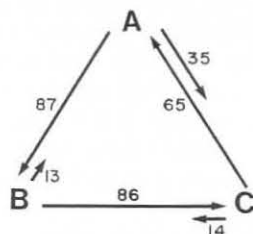
The Cost of Competition

Although overgrowth rankings provide a simple assessment of winners and losers at a particular time, a third level of analysis of competition—the assessment of the cost of engaging in a competitive encounter—is not revealed by these rankings. To measure the costs of competition, one must assess the risk of death or reduced potential for growth and fecundity of both the overgrowing and the overgrown colony. Such data are rare.

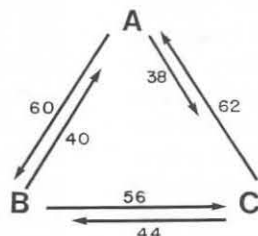
Overgrowth may result in the death of the overgrown colony. For example, colonies of the colonial hydroid *Hydractinia echinata* compete for space on hermit crab shells, and competition typically results in the demise of one of the two competing colonies (Ivker 1972, Buss and Grosberg in preparation). The cost to the victor of engaging in such an encounter in terms of growth and reproductive output varies as a complex function of the relative sizes and competitive abilities of the interacting colonies (Buss and Grosberg in preparation). Far more frequent than actual colony death is the interruption of growth and reduction in colony size by overgrowth. For example, Ayling (1983) monitored overgrowth interactions among encrusting demosponges for a period of nine months and found no cases in which overgrowth led to colony death or even appreciable capture by the overgrowing species of the space occupied by the overgrown species. In contrast to the hydroid example, overgrowth in this system appears to have only a modest effect on survivorship, but rather seems to act to limit the area occupied and hence the fecundity realized by particular colonies.

One clearly cannot assess the cost of competi-

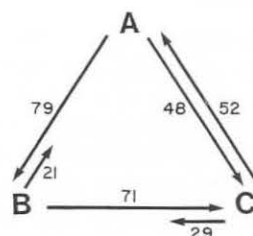
Q. Australian Fouling Panels



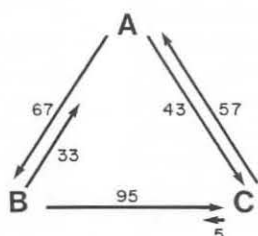
b. Australian Pilings



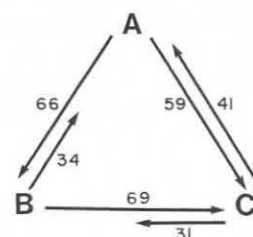
C. Panamanian Cobble



d. British Cobble



e. Washington State Algal Pavements



f. Jamaican Cryptic Coral Reefs

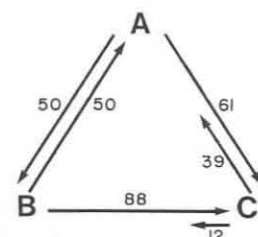


Fig. 31.3 Selected subsets of overgrowth rankings from various marine hard-substratum communities. Arrows point from the dominant competitor to the subordinate. Numbers represent the percentage of total outcomes observed. (a) Australian fouling panels. A = *Distaplia viridis*, B = *Esperiopsis* sp., C = *Botrylloides nigrum*. (Russ 1982.) (b) Australian pilings. A = *Crella* sp., B = *Didemnum* sp., C = unidentified didemnid ascidian. (Kay and Keough 1981.) (c) Panamanian cobble. A = *Antropora tinctoria*, B = *Onychocella alula*, C = *Neogoniolithum rugulosum*. (Buss 1980.) (d) British cobble. A = *Escharella immersa*, B = *Chorizopora brongniartii*, C = *Callopora rylandi*. (Rubin 1982.) (e) Washington State algal pavements. A = *Pseudolithophyllum lichenare*, B = *Pseudolithophyllum whidbeyense*, C = *Lithothamnium phymatodeum*. (Paine 1984.) (f) Jamaican cryptic coral reefs. A = *Steganoporella magnilabris*, B = *Parasmittina* sp., C = *Reptadeonella violacea*. (Jackson 1979b.)

tion from static observations of overgrowth alone. Overgrowth rankings have two severe limitations. First, the observation of overgrowth at a given time may not accurately reflect the eventual outcome of that interaction. The reversal of overgrowth rankings over time between two individuals is well known, and there is no substitute for long-term observations. Second, some taxa are tolerant of epizooism, that is, a colony may survive being overgrown for an extended period and will recover should some other process remove the successful competitor. The recovery of an overgrown colony may represent the ability of tissues to remain viable while overgrown or, more frequently, may represent the ability of not yet overgrown tissues in the colony to recapture the ground previously yielded to the competitor. Hence, static observation of competition does not allow assessment of either the eventual outcome or the potential severity of a particular interaction.

While the cost of competition in terms of reduced growth, fecundity, and survivorship can be empirically determined, these costs are not the only ones associated with interference competition. Successful competitors are often characterized by morphological or physiological modifications that are central to their ability to overcome others in combat (Case and Gilpin 1974). Such "fixed costs" are often exceedingly difficult to quantify, if these modifications are features that serve roles in addition to their function in competition. There are some structures that are used only in competition (see the later section on mechanisms of competition), and in these cases fixed costs are potentially easier to quantify. In either case, however, a precise understanding of the costs of competition must reveal the compromises between potential for growth and reproduction and capacity for intra- and interspecific competition that these morphological and physiological modifications involve. This ultimately requires an understanding of the genetics of the traits and the manner in which their expression is differentially regulated.

Resource Structure and Renewal

A thorough understanding of the nature of competition requires an appreciation of the structure

of the resource and its pattern of renewal. Space for marine hard-substrata organisms occurs as a series of habitable areas that are physically discontinuous and separated by the uninhabitable media of water and soft substrata. Stretches of rocky shore along a coast are separated by stretches of sandy beach, reefal structures are separated by sand channels, and boulders, cobbles, and shell fragments are separated by water, mud, or sand. The sessile nature of the fauna makes each such unit a system closed to communication with other similar units except by exchange of propagules capable of dispersal over considerable distances. On all but the largest substrata (e.g., rocky shores), the number and type of propagules that arrive on a particular unit differ from those arriving on other units, with profound effects on the subsequent development of the fauna on that particular substratum (Sutherland 1974, 1976, 1977, 1978; Menge and Sutherland 1976, Jackson 1977b, Osman 1977, Sutherland and Karlson 1977).

In addition to the resource's structure, one must also consider its generation or renewal, whether as whole units or as patches within a unit. Generation of space has been extensively investigated on rocky shorelines, where patch production is the primary form of resource renewal (Paine and Levin 1981). However, generalizing these results to other marine hard grounds is not entirely appropriate, as space-generating processes operate on different spatial and temporal scales in different environments. For example, in rocky intertidal environments new discrete substrata, that is, new stretches of shore, appear only on geological time scales, whereas patches appear at a far more rapid rate. New coral reef surfaces may arise every 30 or 40 years following a major hurricane, and space is generated both by generation of these substrata and of patches within the substratum. At the opposite extreme, relatively small discrete substrata are renewed even more rapidly through simple introduction of new substrata, such as a new shell or cobble.

Correlates of Competitive Success

Given a knowledge of the frequency at which a species wins or loses a particular interaction, a

fifth level of analysis of competition may be profitably explored: determining the ecological correlates associated with competitive success. Considerable progress has been made in this direction, especially in documenting changes in competitive ability as a function of the life history stages involved in the interaction. Three examples follow.

Size In tidal channels on the rocky shore of Punta Paitilla, Panama, small cobbles accumulate. These cobbles are dominated by three encrusting, clonal organisms at midtidal levels, the encrusting cheilostomatous bryozoans *Antropora tinctoria* and *Onychocella alula* and the coralline alga *Neogoniolithum rugulosum*. Studies of the overgrowth relationships among these three species show that no clear competitive dominant exists (Fig. 31.3c). *A. tinctoria* wins most of its interactions with *O. alula*, *O. alula* wins most of its interactions with *N. rugulosum*, and *N. rugulosum* wins slightly over half its interactions with *A. tinctoria*. All three species are skeletonized organisms without the capacity to lift their growing margins above the substratum that they encrust. As such, thicker colonies generally overgrow thinner ones and thickness is related to colony area (Buss 1980). Thickness increases proportionately with surface area for *A. tinctoria* and *N. rugulosum*, but is a constant for *O. alula*.

A discriminant function was calculated in an attempt to predict competitive outcome based solely on knowledge of colony area. This analysis demonstrated that no less than 75% of all outcomes between these three species were correctly predicted on the basis of colony size alone. Colony size is an excellent predictor of competitive ability in this and several other interactions (e.g., Connell 1961a, Day 1977, Russ 1982).

Density The cheilostome bryozoans *Bugula turrita* and *Schizoporella errata* are numerically important components of fouling communities along the Atlantic coast of North America. *B. turrita* is a lightly calcified arborescent anascan and is readily pushed over and overgrown by the heavily calcified encrusting ascophoran *S. errata*. Despite this clear dominance of *S. errata* over *B. turrita* in overgrowth encounters, *B. turrita* is an abundant organism, often occurring in dense associations of numerous uprights.

The persistence of dense associations of *B. turrita* uprights in the face of *S. errata* competitive dominance led me to study the mechanism of aggregate formation, the effect of intraspecific competition on the growth of uprights within an aggregate, and the effect of interspecific competition with *S. errata* as a function of *B. turrita* density (Buss 1981a). Results of laboratory habitat selection experiments show that *B. turrita* recruitment is strongly density- and size-dependent; larvae selectively choose habitats in which density of new recruits is high, leading to the establishment of dense monospecific stands (see also Keough 1984). Growth rates of *B. turrita* colonies are strongly influenced by density, with growth stunted at high density, presumably due to intraspecific competition. In contrast to the results of intraspecific competition, growth of *B. turrita* in interspecific competition with *S. errata* is positively associated with *B. turrita* density. Dense populations of *B. turrita* are rarely overgrown by *S. errata*, whereas solitary individuals are uniformly overgrown. In this case the outcome of interspecific competition is strongly density-dependent.

Growth Morphology In temperate soft-bottom environments worldwide, colonies of the athecate hydroid *Hydractinia* live symbiotically on the shells of hermit crabs of the genus *Pagurus*. Colonies of *H. echinata* vary considerably in colony morphology, and this variation has a strong genetic component (McFadden et al. 1984). Some individuals develop as a uniform sheet of ectodermal mat, overlying an extensive gastrovascular canal system. Other colonies develop differing degrees of stolonal extensions (that is, single periderm-covered gastrovascular canals) from the centrally placed mat, with some colonies producing a complex network of anastomosing stolons crisscrossing the substratum (Fig. 31.4).

This variation in growth morphology has important implications for intraspecific combat, because mat and stolonal tissues differ in their morphogenetic potential for producing those tissues required for aggression (Buss et al. 1984). When mat tissue comes into contact with mat tissue, active aggression does not occur; rather, colonies simply cease growth along the interactive

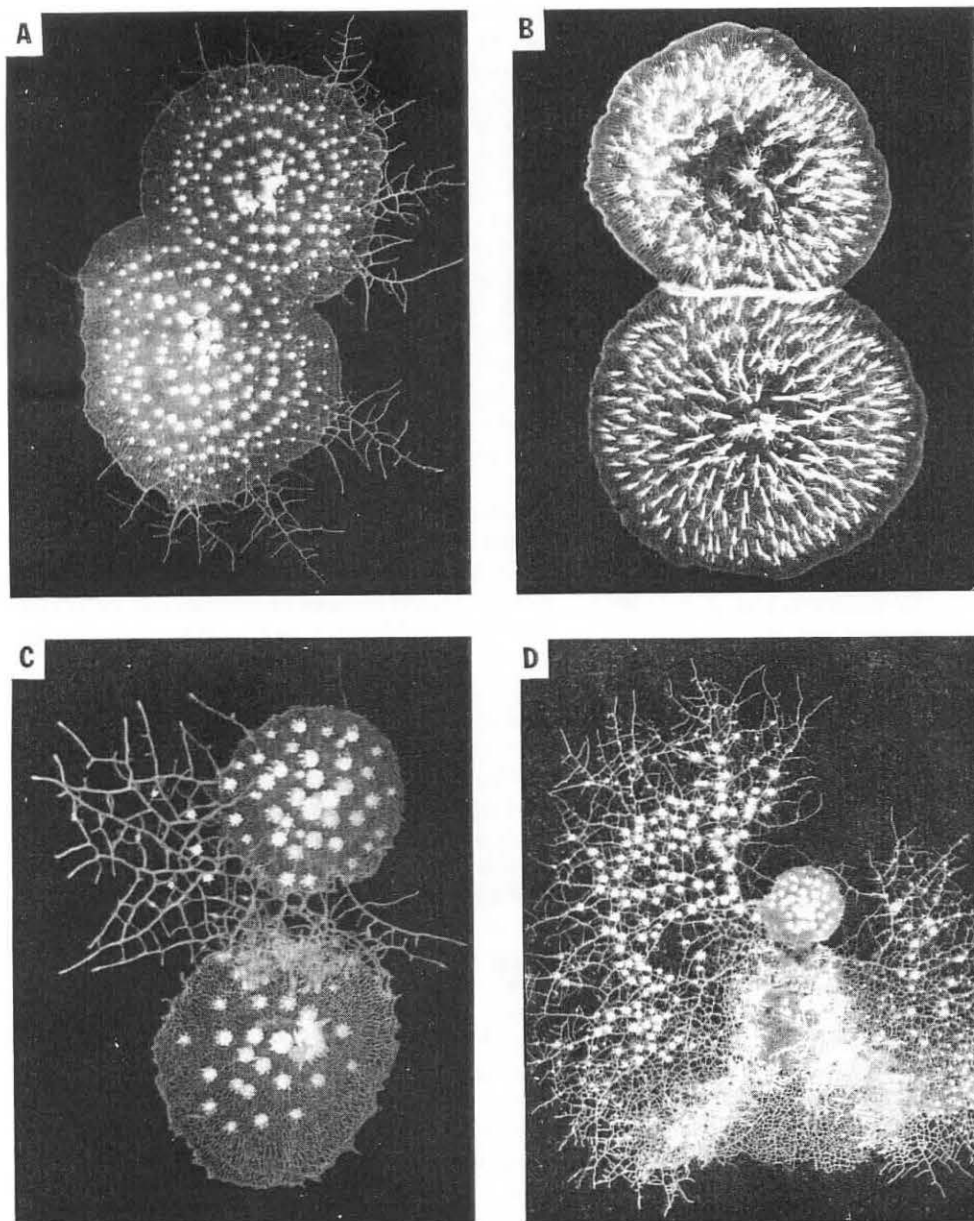


Fig. 31.4 Intraspecific competition between colonies of the colonial, athecate hydroid *Hydractinia echinata*. (A) Fusion between colonies, showing the result of intraspecific contact between histocompatible colonies. (B) Competition without aggression. These stolonless colonies do not fuse; they simply cease growth along the interactive margin. (C) Competition with aggression. The stoloniferous colony (upper) is developing hyperplastic stolons where it contacts the ectodermal mat of the stolonless colony (lower). (D) Competition with aggression. In this interaction between two stoloniferous colonies the upper colony has developed extensive hyperplastic stolons along its zone of contact with the lower colony and has almost completely overgrown it.

margin (Fig. 31.4B). In contrast, when stolons contact foreign tissue, they hypertrophy, lift off the substratum, and effect the destruction of the foreign colony (Figs. 31.4C and 31.4D). The differing morphogenetic potential of the two tissue types results in a strictly deterministic relationship between growth morphology and competitive ability; stoloniferous colonies always overcome less stoloniferous or matty colonies in pairwise symmetrical encounters (Buss and Grosberg in preparation).

Mechanisms of Competition

The final level of analysis of competition is the elucidation of the mechanism of the interaction. That analysis may proceed at a variety of levels. Phenomenological examination of overgrowth interactions may lead to the clear association of certain traits of an organism with different overgrowth results. Examination of such interactions in detail may lead to an understanding of the cellular and subcellular basis of one organism's ability (or inability) to overcome another organism. Studies of the transmission and molecular genetics will ultimately identify the arrangement of competition genes and elucidate their potential for evolutionary modification. Although considerable progress is being made, we are far from any such thorough analysis for any competitive interactions among sessile clonal organisms. Nevertheless, an understanding of mechanism is important if we are to (1) quantify precisely the costs of competition, (2) determine the degree to which ecological circumstance can result in plasticity in competitive ability, (3) determine the extent and control of compromises between competitive ability and growth or reproductive output, and (4) understand the evolutionary potentials for aggression within and between different taxa.

Below I summarize known mechanisms of competition in two groups of common sessile organisms, the encrusting cheilostomatous Bryozoa and the polypoid life stages of Cnidaria. Interactions between individuals within each group are certainly among the best-known examples of interspecific competition among clonal marine invertebrates.

Bryozoa Cheilostomatous bryozoans are skeletonized encrusting organisms that are generally unable to effect the destruction of foreign tissues

over a distance. Bryozoans grow as a lineal series or radial arrangement of adjacent lineal series of asexually iterated calcified zooids (see Fig. 31.1). Growth is typically restricted to the margins of a colony. For organisms of this sort, overgrowth mechanisms involve structural features that act to influence either the relative vertical relief of two interacting colonies or the relative rates of lateral and vertical growth along the interactive margin.

A number of encrusting bryozoans have evolved structural modifications on this basic growth plan that allow them to reposition their growing margins in ways that fundamentally alter their competitive abilities (Stebbing 1973; Jackson and Buss 1975; Jackson 1979a, 1979b; Buss 1981a, 1981b; Lidgard and Jackson 1982). Some bryozoans are capable of producing new zooids on top of preexisting ones, a process called frontal budding. This trait allows a colony to reposition the growth margins at considerable distances from the basal layer of zooids. The trait is clearly associated with overgrowth success in competition against species that have no similar capacity to alter the vertical position of their growing margins. Several species of bryozoans are capable of another budding pattern, that of simultaneously producing several immature zooids, or giant buds, along a growing margin. Giant buds allow a colony to achieve a faster rate of lateral growth than a similarly calcified colony that buds zooids one at a time. Giant buds are associated with overgrowth success, especially when combined with a third trait, the capacity to grow marginal zooids unattached to the underlying substrata (Fig. 31.1). The capacity to lift locally off a substratum clearly allows a colony considerable capacity for modifying the vertical relief of its growing surface relative to a substratum-bound competitor. The phyletic distribution of these three traits, along with various others relevant to overgrowth success, suggests that these patterns have evolved convergently in a large number of cheilostome families (Lidgard and Jackson 1982).

Species and individual colonies vary considerably in the degree to which these devices are deployed. For example, a colony may grow giant buds only along a portion of the colony, or frontally budded layers may be restricted to certain regions of the colony (Jackson 1979b). It is the variability in the expression of these morpholo-

gies at various points along the colony margin that gives rise to the extraordinary variability in overgrowth rankings among bryozoans and the repeated observation that overgrowth results among bryozoans are correlated with encounter conditions (Jackson and Buss 1975; Jackson 1979b; Buss 1980, 1981b; Rubin 1982). Unfortunately, the study of the various budding patterns associated with competitive success among the Bryozoa have been limited almost exclusively to studies at a phenomenological level; little is known of the cellular and subcellular basis for differing growth patterns, and genetic data are entirely lacking.

Cnidaria In contrast to bryozoans, where competition is often mediated by permanent structural features, many cnidarians are capable of the temporary induction of specialized tissues that respond to intra- and interspecific competition and that destroy foreign tissues. An example of such an interaction was introduced earlier, that of encounters between colonies of *Hydractinia echinata* (Fig. 31.4). When stolons of opposing colonies encounter one another, the stolons differentiate into a new structure, called a hyperplastic stolon (Ivker 1972, Buss et al. 1984). These hyperplastic stolons, which appear only when a colony interacts with another hydractiniid hydroid, are formed by the movement of multipotent interstitial cells from the central mat region into the stolons (Figs. 31.5 and 31.6). The interstitial cells differentiate into mature nematocytes, cells containing harpoonlike organelles called nematocysts (Buss et al. 1984). Nematocysts are used in prey capture and are typically armed with potent toxins (Mariscal 1974). Upon contact with the foreign colony the nematocyst batteries of the hyperplastic stolon discharge into the foreign tissue, destroying it (Figs. 31.5 and 31.6).

Interactions of this sort are not limited to hydractiniid hydroids (see Buss et al. 1984, Table 1). Particularly among anthozoans, there are a diversity of inducible structures that inflict damage on neighbors. Scleractinian corals are capable of differentiating sweeper tentacles, elongate tentacles armed with a distinct nematocyst population (Richardson et al. 1979, Wellington 1980, Chornesky 1983). Certain anemones display an analogous phenomenon. Upon contact

with neighbors these anemones differentiate catch tentacles armed with a specialized nematocyst population and used to destroy foreign tissues (Williams 1975, Purcell 1977, Watson and Mariscal 1983). Other anemones deploy an entirely different structure. The body columns of these species possess batteries of nematocysts in structures called acrorhagi, which upon contact with neighbors can inflate, reach out, and discharge their nematocysts into foreign tissues (Francis 1973, Williams 1978, Ottaway 1978, Bigger 1980, Brace 1981). It is indeed striking that such a diverse array of specialized, induced structures have evolved to deploy the same nematocyst-based effector system.

The study of competition among cnidarians has revealed an association between the deployment of competitive mechanisms and the capacity for historecognition (see Fig. 31.4A). It is commonly assumed that competition and historecognition are genetically based alternatives in Cnidaria, although genetic data are available only for *Hydractinia echinata* (Hauenschild 1954, 1956; Ivker 1972). The assumption is justified on the basis of the repeated observation that competition occurs only between unrelated individuals or species and that aggression is not observed between related individuals or clone-mates (see review by Buss 1982).

The association of competition among cnidarians with historecognition holds great promise for a more complete description of these interactions on a mechanistic level. If the genetic complexes coding for historecognition in cnidarians are homologous to those coding for historecognition in vertebrates, the opportunities for molecular genetic analysis are enormous. The increasing availability of cDNA clones to various regions of the mouse major histocompatibility complex should allow this study to be pursued. An understanding of cnidarian competition based on data from the community, populational, developmental, cellular, and ultimately molecular-genetic levels may well be possible in a relatively short time.

ON FAILING TO OBSERVE COMPETITION

Just as competition occurs chronically in a number of marine, hard-substratum environments, so

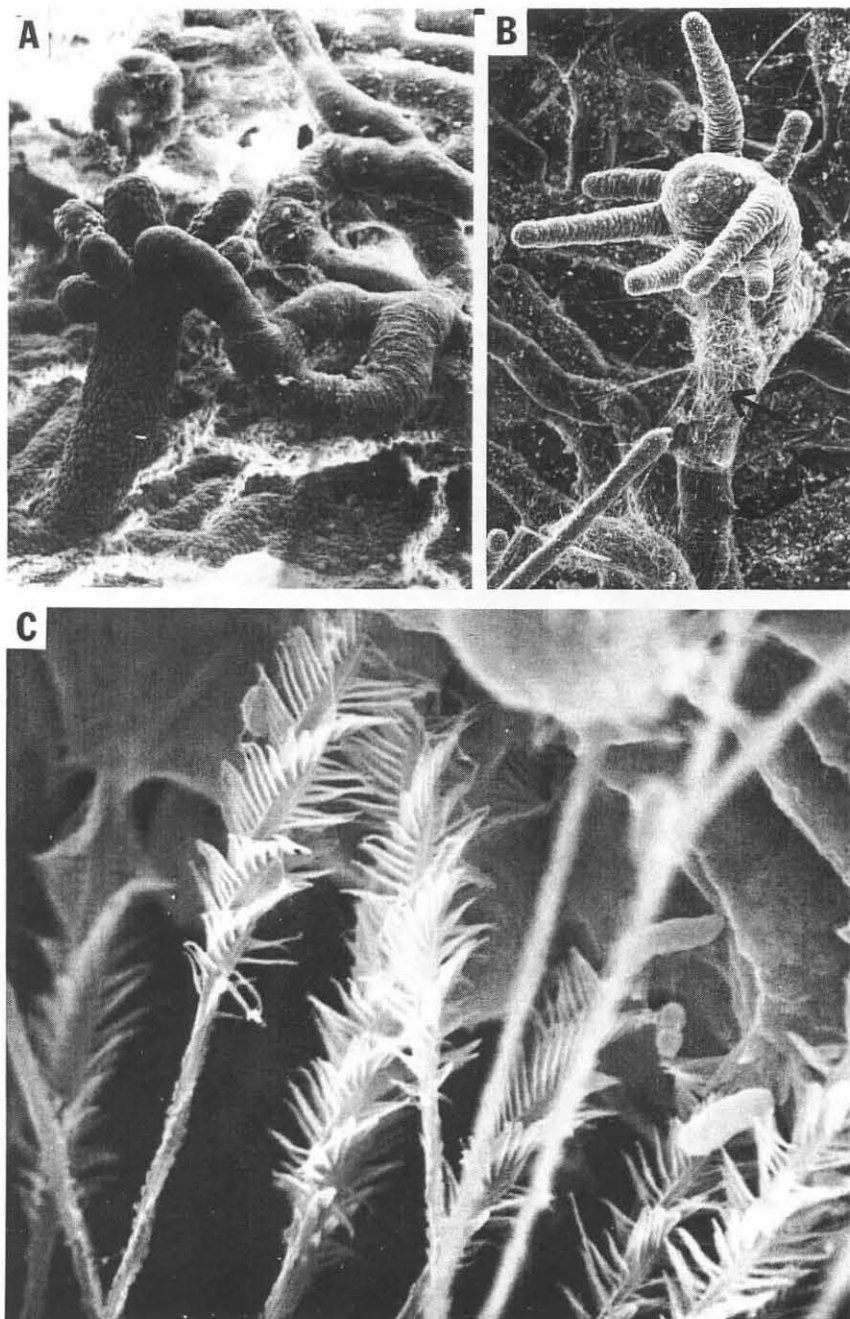


Fig. 31.5 Details of the competitive mechanism of hydractiniid hydroids (A) Scanning electron micrograph showing a hyperplastic stolon arching off the substratum toward a polyp of its competitor ($106\times$). (B) Contact between a hyperplastic stolon and the polyp of a competitor ($167\times$). Note the concentration of nematocyst threads where the hyperplastic stolon contacts the polyp of the competitor. (C) Discharged basotrichious isorhizal nematocysts extending from a hyperplastic stolon ($387\times$). (Buss et al. 1984).

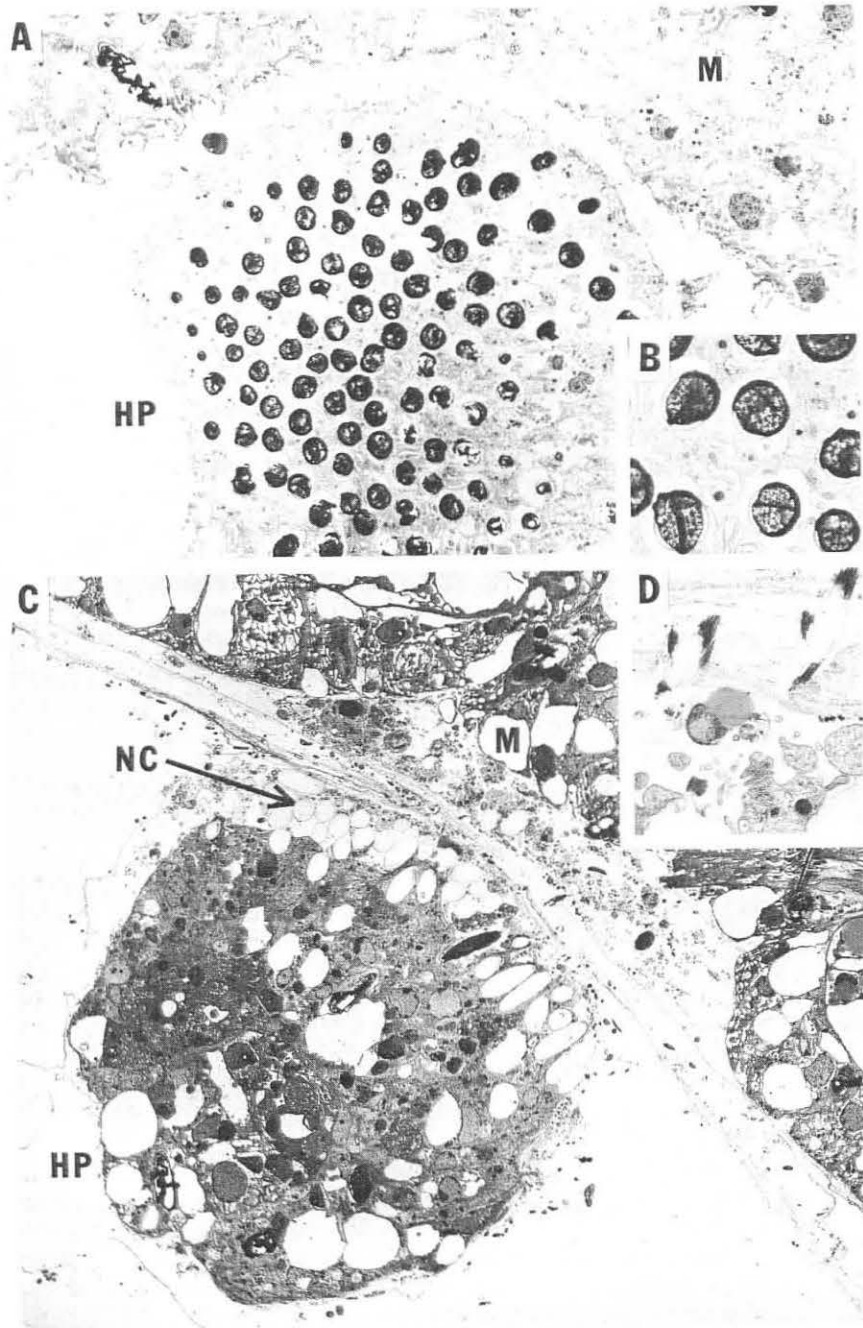


Fig. 31.6 Details of the competitive mechanism of hydractiniid hydroids. HP = hyperplastic stolon; M = ectodermal mat of competitor; NC = nematocyst capsule. (A) Transmission electron micrograph across the tip of a hyperplastic stolon in contact with a competitor ($700\times$). Note that almost every cell harbors a nematocyst. (B) Part of section shown in A at greater magnification ($2,880\times$). (C) Section across a hyperplastic stolon in contact with a competitor ($704\times$). Capsules of discharged nematocysts are concentrated along the margin of the hyperplastic stolon where it is in contact with its competitor's tissue, and there is a zone of necrosis directly underlying this region. These discharged capsules are eventually sloughed off, a new set of nematocytes is differentiated, and the interaction is repeated until one colony has been completely eliminated. (D) The contact zone in C at greater magnification ($2,880\times$), showing shafts of the nematocysts embedded in the foreign tissue. (Buss et al. 1984.)

does predation. The manner in which these two processes interact to produce patterns of distribution and abundance is clearly of fundamental importance. Since the publication in 1966 by Robert Paine of the predation hypothesis, many marine ecologists have focused on the suggestion that "local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites by one species" (Paine 1966). The predation hypothesis has motivated an enormous amount of experimental work, mostly concentrated in the marginal marine environments (such as rocky shorelines), and is one of the few ecological suggestions based on solid experimental data, repeated several times, and in several places (e.g., Paine 1966, 1971, 1974; Paine and Vadas 1969; Harper 1969; Dayton 1971; Menge 1976; Lubchenco 1978, 1980; Lubchenco and Menge 1978; Sousa 1979).

The predation hypothesis holds only that "diversity is directly related" to the control of resource monopolization by predation or disturbance. The manner in which it is related has been and continues to be a topic of considerable research interest (see the following section on reconciling the predation hypothesis with observations of competition). One such relationship is that predation acts to preclude the occurrence of interspecific competition by holding structurally or numerically important prey species to densities at which interspecific competition fails to arise (Paine 1966). In this case predation and interspecific competition are mutually exclusive processes [but note that in such a case competition may yet occur between taxa of another morphological scale (Paine personal communication)]. If hypotheses are to be constructed to define the conditions under which competition will or will not be observed in nature, it is necessary to identify clearly the conditions under which predation can preclude the occurrence of competition.

Under what conditions will competition persist in the face of predation? At least five conditions may mitigate against predation precluding competition. Several of these limitations have been noted by others (Chapter 30: Dayton 1971, Connell 1975, Jackson 1977a, Lubchenco and Gaines 1981) and are treated only briefly here. Lubchenco and Gaines (1981) have divided these

conditions into two categories: those in which predators and prey will coexist microsympatrically and those in which predator and prey will not coexist. In their classification conditions 1, 2, 3, and 5 (below) would permit coexistence, conditions 3 and 4 preclude coexistence

1. Settlement The relationship between a predator and its dominant prey is sensitive to variation in the density of both predator and prey. For example, Dayton (1971) attempted to repeat Paine's (1966) classic experiments on the effect of the predatory starfish *Pisaster* and failed. This failure was attributed to the failure of the competitively dominant mussel to recruit in sufficiently high densities that year (Dayton 1971, Paine 1974). Abundant evidence suggests that predation will act to preclude competition under only a restricted range of densities (Chapters 29 and 30; Dayton 1971; Yodzis 1978; Denley and Underwood 1979; Underwood et al. 1983; Underwood and Denley 1984; Roughgarden, Iwasa, and Baxter 1985).

2. Predator Resistance Even in the face of high predation pressure, some prey species typically escape predation through chemical, structural, or size-related antipredatory traits. Many such prey species are dependent on the predator, in that they are competitively inferior to species more susceptible to predation (Lubchenco and Gaines 1981, Steneck 1982). If two or more species prove predator-resistant and if recruitment is sufficiently great, predation will not act to preclude competition between the resistant species.

3. Predator Limitation Predators that might otherwise be capable of reducing competition between prey may be prohibited from doing so in some regions by physiological limitations or by reductions in their densities by their own predators (see reviews by Connell 1975, Lubchenco and Gaines 1981).

4. Refugia If predation pressure is sufficiently intense and chronically so, prey species may be forced to compete for refugia (see examples for freshwater fish and herbivorous insects in Chapters 21 and 31; Lubchenco and Gaines

1981, Fig. 4). Imagine two species that in the absence of predation reach high densities and compete for food. If predation is introduced, prey density may drop sufficiently that such interspecific competition no longer occurs. If, however, predation intensity increases yet further, competition may again become important in that prey may be driven to compete for refugia. Predation, if sufficiently intense and chronic, may act to change the resource that is limiting, in this case, from food or space to refugia. As long as the density of prey seeking refugia is greater than the availability of the refugia, competition will occur. Competition for refugia in the face of predation may well be a condition occurring quite frequently among mobile organisms whose foraging habits or breeding habits require that they be active at the same time as predators.

5. Clonality If predation is to preclude competition, it must either reduce the density of potential competitors seeking a limited resource or increase the availability of the resource at a rate faster than the demographic characteristics of the prey allow its exploitation (or both). The act of predation, though, need not result in an immediate reduction in prey density. In fact, predation on established clonal organisms rarely results in the death of the predated individual (Jackson 1977a). Rather, predators only open a patch within the clone which may either be immediately recaptured by regeneration or be captured by recruits. In the former case, the act of partial predation may have no immediate effect on competition. In the latter case, the capacity for clonal growth ensures that the originally predated clone will soon encounter the recruit, hence actually increasing the frequency of competition. Clonal propagation is a demographic character that will frequently allow a clone not only to escape predation, but also rapidly to recapture resources lost to predation. If prey are routinely capable of recapturing the resource freed by the loss of ramets to predators, predators will not necessarily act to preclude any existing competition between prey.

The failure of predation to preclude the occurrence of competition among clonal organisms needs no special demonstration. An encrusting coral colony that has a portion of its center eaten

by a sea urchin is no less in competition with a sponge or another coral along its colony margin. The importance of clonality should not be underestimated. The overwhelming majority of the subtidal hard substrata in the sea are dominated by clonal groups (Jackson 1977a, 1983). Furthermore, a large percentage of lower trophic levels in terrestrial communities are clonal, including most grasses and herbs (Harper 1977). In addition, prey need not be clonal for predation to fail to influence density. A tree suffering aphid predation may nonetheless be faced with competition with a liana. As long as the portion of the prey consumed is an iterated unit, which the prey can either regenerate or bud anew (for example, the first several segments of an annelid), predation may also fail to have an immediate impact on prey density (Woodin 1982).

The routine failure of predation to reduce prey density in clonal groups should not be taken to suggest that predators are uniformly unable to reduce prey density. Predators may reduce prey density in clonal groups (1) if they feed primarily on dispersal units (such as in seed predation) or eliminate clones when small, (2) if predator density is sufficiently great, as when the crown-of-thorns starfish devastated acroporid reefs in certain Indo-Pacific islands, or (3) if predation reduces the viability of the clone sufficiently to increase the susceptibility of the colony to further predation or other threats. Nevertheless, these effects are often not sufficient to preclude prey from reaching densities at which they compete, as evidenced by the routine observation of competition among clonal, marine, sessile invertebrates (Jackson 1977a).

These five types of limitations, however, do not necessarily dilute the generality of the predation hypothesis. The predation hypothesis in its original form requires only that predation be "directly related" to prevention of resource monopolization (Paine 1966). For present purposes the hypothesis may be divided into two cases: one in which competition occurs and another in which competition does not occur. The conditions under which predation does not preclude competition are potentially quite frequent ones. The persistence of competition in the face of predation is an area of considerable recent work in marine systems and the subject of the remaining discussion.

RECONCILING THE PREDATION HYPOTHESIS WITH OBSERVATIONS OF COMPETITION

The predation hypothesis holds that predation is directly related to the prevention of resource monopolization. The manner in which it is related has proved to be rather complex. At least two patterns (see Chapter 29 for discussion) are known from experimental removal of predators in the field. (1) Increasing predator intensity may first increase local diversity to a maximum at some intermediate level and may act with further increases to decrease diversity; (2) increasing predation may act to decrease diversity in a monotonic fashion (e.g., Paine 1966, 1971, 1974; Paine and Vadas 1969; Harper 1969; Connell 1978; Lubchenco 1978). A number of authors have suggested that predators can increase diversity only when the predator feeds preferentially on that prey that is the clear competitive dominant (e.g., Paine 1966, 1971; Harper 1969; Hall et al. 1970; MacArthur 1972a; Lubchenco 1978).

Most experimental studies of predation and community organization are based on studies in the rocky intertidal. Unfortunately, data on the relative competitive abilities of intertidal sessile organisms are incomplete. Typically, competitive dominance in the intertidal is treated as synonymous with numerical dominance in the absence of predation (e.g., Paine 1966). While the relative competitive abilities of some subordinate species in these systems have been analyzed experimentally (Connell 1961a, Wethey 1984), most competitive abilities are either unknown or inferred from natural history observations.

Nevertheless, the hypothesis that feeding preferences and competitive rankings of prey in a largely transitive competitive series jointly determine whether diversity falls monotonically with predation or else rises and then falls was tested by Lubchenco (1978). She performed an elegant series of experimental manipulations of the introduced herbivore *Littorina littorea* on various algal prey. In this system the relative competitive abilities of the algal species are apparently reversed in different environmental settings: the perennial red alga *Chondrus crispus* is dominant on exposed surfaces, whereas the ephemeral alga

Enteromorpha intestinalis is dominant in tidal pools. Exploiting this competitive reversal in different habitats, Lubchenco manipulated the density of prey and obtained a striking result: diversity decreased monotonically with increasing predator pressure if competitive subordinates were the preferred prey, while diversity showed a maximum at intermediate predation levels if predators preferred the competitive dominant.

In the *Littorina* system a clear competitive dominant was apparent in each habitat type. In a number of other systems, however, overgrowth (dominance) rankings fail to allow the simple identification of a single competitive dominant (Fig. 31.3), raising the question of how predation interacts with competition in these systems. Jackson and Buss (1975) proposed that intransitive competitive relationships would strongly influence the rate at which resources are monopolized by a single species. Specifically, we suggested that the more intransitive the competitive ranking, "the slower will space tend to be occupied by a single competitive dominant, and [hence] the less the amount of external disturbance necessary to maintain a given level of diversity." Simulation studies of this amended hypothesis substantiate this prediction (Karlson and Buss 1984).

The basis for this suggestion is quite simple. Imagine a surface occupied by three encrusting colonial organisms. If the competitive relationships of these three species are purely transitive, the dominant will simply expand to cover the space occupied by its neighbors. If, however, the system is intransitive, each species will lose some ground along one region of its margin and gain ground in others. While it is clear that in the absence of disturbance a single dominant will eventually emerge in such a system (except under the biologically unrealistic condition that overgrowth rates are identical for all species), it is similarly clear that the rate at which the resource is monopolized by a single species will be far slower than for a comparable transitive system (see Buss and Jackson 1979, Figs. 5–7). This suggestion has been further investigated in simulation studies, which confirm that the time required for resource monopolization by a single species is highly sensitive to variation in competitive rankings and in rates of overgrowth (Karlson and Jackson 1981).

How, then, is predation related to diversity in intransitive systems? Given the extraordinary sensitivity of single species resource monopolization rates to relative overgrowth rates and the effect that partial predation on clonal organisms is likely to have on their growth rates, one might expect that predation might interact with competition by modifying overgrowth (or dominance) relationships. I know of only two studies that directly address this question (but see Park 1948, Steneck 1982), and I shall summarize both. One study used Panamanian cobble, and the other used Washington coral algal pavements.

Panamanian Cobble

As described earlier, cobbles in tidal channels at Punta Paitilla, Panama, are commonly dominated by two sessile encrusting cheilostome bryozoa and a coralline alga. Both static and time-course observations of overgrowth relationships among these species are highly intransitive (Fig. 31.2c). The three species occur in midintertidal channels, which I interpret (in the absence of experimental data) to mean that the channels are sandwiched between a higher zone in which thermal stress excludes bryozoans and a lower zone in which anascan bryozoans are largely replaced by ascophorans. These channels are characterized by an enormous diversity of potential predators, including a diverse gastropod guild. Species capable of completely removing the entire sessile encrusting community, such as cowries or urchins, cannot survive in these pools due to thermal stress. In addition to the gastropod predators the cobbles harbor a population of the isopod *Paraleptosphaeroma glynni*, a form known to occur only in association with the two bryozoan species (Buss and Iverson 1981). The isopod preys on the bryozoan species, one zooid at a time. Although the isopod preys on both bryozoans, small isopod individuals are more frequent than large individuals and can prey only on the faster growing species, *Antropora tinctoria* (Buss and Iverson 1981).

To determine the impact of isopod predation on the competitive relationships in the sessile community and on the maintenance of diversity in this system, I experimentally removed isopods from 25 cobbles and followed the fate of the encrusting community relative to 25 control cob-

bles. The removal process involved collecting the cobble bimonthly and cleaning the surface with a Water Pik. The isopods blown off in this process were removed and the remaining fauna (including juvenile gastropods) were allowed to repopulate the cobble. Controls were treated in the same fashion, except that isopods were also allowed to repopulate cobbles. The removal process was more than 95% effective. Isopods rarely recruited to the isopod-removal rocks because *P. glynni* lacks swimming appendages.

The results are: (1) The removal of the isopod predators leads to a reduction in diversity from the original three-species condition to a one-species system dominated by the fastest growing species, *Antropora tinctoria* (Fig. 31.7). (2) The manner in which this domination is achieved is mediated through a change in the dominance (overgrowth) rankings of the sessile community (inset, Fig. 31.7). Shortly after the initial removal the number of cobble on which competitive rankings remained intransitive decreased dramatically. Since the feeding rate of isopods alone is inadequate to account for the dominance of *A. tinctoria* (compare data in Buss 1981b and Buss and Iverson 1981), the isopods must have acted to influence the competitive ability of the fastest growing species relative to the two slower growing species, maintaining intransitivity, and reducing the rate at which the *A. tinctoria* achieved dominance. The transition from intransitivity to transitivity in this experiment is not a surprising result. Any multispecies space-limited competitive situation involving encrusting organisms, whether transitive or intransitive, will eventually lead to single species monopolization in the absence of disturbance, except in the biologically unrealistic condition of intransitivity with exactly equal rates of overgrowth (Jackson and Buss 1975, Buss and Jackson 1979, Karlson and Jackson 1981, Karlson and Buss 1984).

Washington State Coralline Algal Pavements

Paine (1984), reporting on collaborative work with Robert Steneck currently in progress, describes a similar pattern emerging in studies of coralline algal pavements on intertidal surfaces in

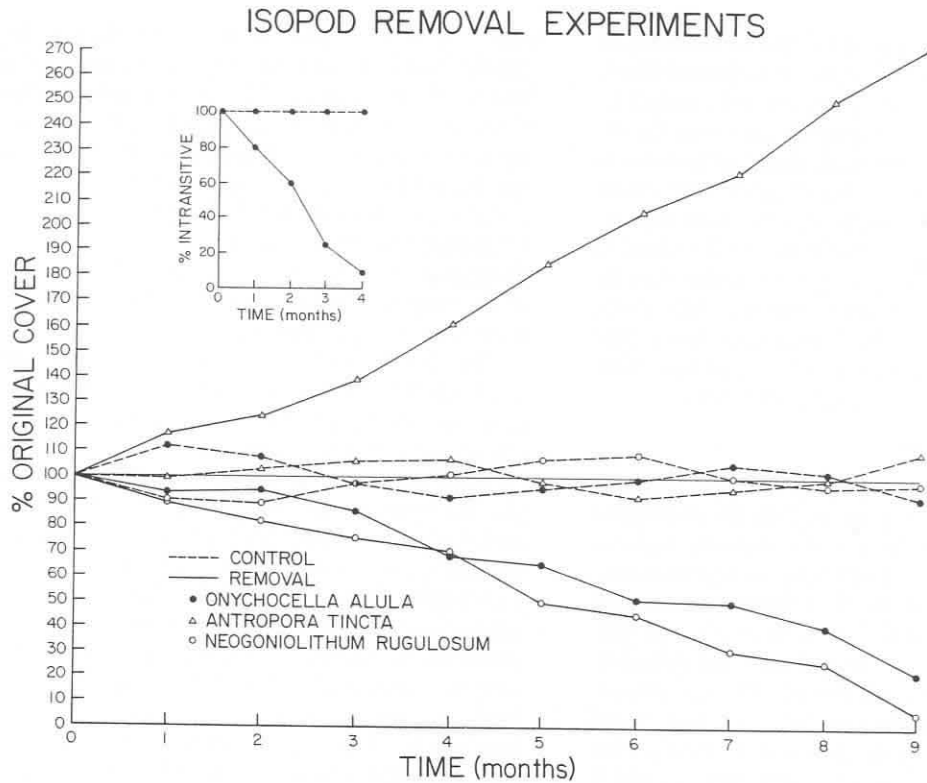


Fig. 31.7 Isopod removal experiments. Data are presented as means of the original cover for 25 control and 25 removal rocks. *Antropora tinctoria* comes to dominate isopod-removal rocks, whereas control rocks maintain all three species. Within four months of the original removal the competitive ranking on all substrata had shifted from highly intransitive to strictly transitive.

Washington State. Coralline algae are clonal plants that encrust surfaces and compete through overgrowth (Steneck 1982). Static overgrowth interactions are highly intransitive (Fig. 31.8). Corallines are routinely capable of persisting in the face of predation, and these particular species are exposed to activities of numerous herbivores, most commonly the chiton *Katharina tunicata* and the limpets *Acmaea mitra* and *Collisella pelta*.

Paine (1984) and Steneck experimentally reduced the density of predators and observed overgrowth rankings in unmanipulated control sites and predator removal sites (Fig. 31.8). In the absence of predators the overgrowth relationships of 1 of the 5 species treated (2 of 10 possible interactions) changed dramatically. Prior to the removal *Lithothamnium phymatodeum* (species B in Fig. 31.8) overgrew *Pseudolithophyllum whid-*

beyense (species C in Fig. 31.8) in only 33% of their interactions and overgrew *Lithophyllum impressum* (species D in Fig. 31.8) in 40% of their interactions, whereas subsequent to the removal, it was 98% and 100% successful, respectively, in these same interactions. Both of these shifts in dominance increased the transitivity of the overall dominance rankings in the system. The implication here is identical to that described above: predators modify existing competitive relationships, acting to decrease the incidence of transitivity in dominance relationships.

In addition to these experiments Paine (1984) and Steneck established a series of artificial communities and observed overgrowth relationships in the absence of predators. These artificial communities formed almost perfectly transitive competitive rankings in the absence of predation. The results from artificial communities are rather dif-

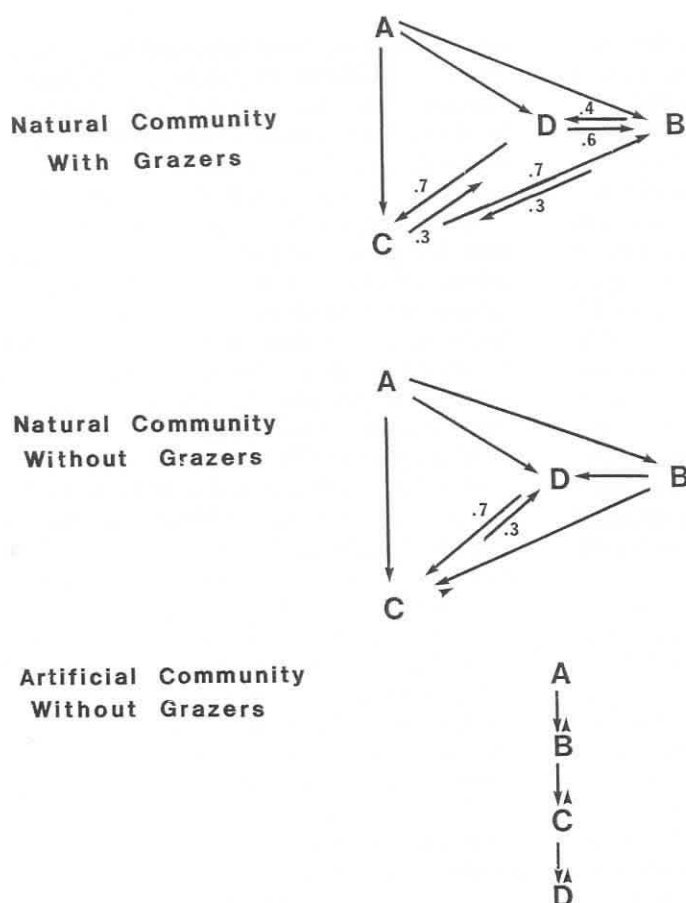


Fig. 31.8 Effect of predator removal on overgrowth relationships within natural and artificial assemblages in coralline algal communities. Arrows point from the winner to the loser. Numbers represent the percentage of total interactions. Competitive dominance was unidirectional, or nearly so, if no number appears. A = *Pseudolithophyllum lichenare*; B = *Lithothamnium phymatodeum*; C = *Pseudolithophyllum whidbeyense*; D = *Lithophyllum impressum*. A fifth species, *Bossiella* sp., is not figured, as it lost all its interactions with all other species in each treatment. (Redrafted from Paine 1984.)

difficult to interpret. These systems were established by chipping off pieces of coralline species and placing them in particular spatial arrangements on the substrata. Although this is a powerful experimental technique, such combats are clearly biased toward symmetrical interactions. On natural substrata thalli contact asymmetrically: some thalli are larger than others, some thalli are thicker than others, some thalli are more shaded than others, and so forth. As discussed earlier in this chapter, there is ample evidence that size, encounter conditions, and morphological variability are correlated with competitive ability. Since the establishment of artificial communities removes environmental heterogeneity (Paine 1984), such systems may be unrealistically simple. Without control artificial communities that include grazers (or without detailed knowledge of

the asymmetries in naturally occurring interactions) the degree to which the establishment of symmetrical communities biases results toward transitivity is difficult to interpret.

Nevertheless, the Panama and Washington studies are fundamentally similar in conclusion. In both cases predation acts on clonal organisms. In both cases predation does not, at least proximately, result in the death of the preyed organism. In both cases predation does not preclude the occurrence of competition; rather, it acts to maintain it. Both experiments are fully consistent with the predation hypothesis (Paine 1966) that "local diversity is directly related to the efficiency at which predators prevent the monopolization of a resource by a single species." Finally, both cases support the original hypothesis that "intransitivity acts to slow the rate of single spe-

cies resource monopolization and to reduce the level of disturbance required to maintain a given level of diversity" (Jackson and Buss 1975).

Thus, predation appears to interact with competition in two quite different ways: (1) Predation reduces or precludes the occurrence of competition in some systems, while (2) predation acts to maintain the occurrence of competition in other systems. The limited data available suggest that the former mode is found in systems with transitive competitive relationships (e.g., Paine 1974; Connell 1978; Lubchenco 1978) and the latter mode in systems with intransitive rankings (Paine 1984). This apparent difference in the manner in which predation and competition interact to produce patterns in community organization raises an important question as to ultimate causes underlying these differences in proximate patterns.

Paine (1984 and Fig. 31.8), however, argues that "the competitive relationships are transitive within this guild of coralline algae," since the removal of predators from an intransitive system results in transitivity. While this perspective has the virtue of defining competitive ability as a function of its consequences in the absence of predation, it has difficulties. Predation is only one process affecting competitive ability (Park 1948). Is it not equally arguable that competitive ability be assessed in the absence of surface irregularities, flow conditions, mutualistic species, thermal tolerances, and so forth? The ability of an organism to withstand predation is every bit as "intrinsic" to an organism as is the ability to withstand thermal conditions. A second, more important difficulty is that this redefinition focuses attention away from the considerable diversity (and interesting biology) of competitive mechanisms employed by sessile plants and animals. I concur with Miller (1967), who, in reviewing Park's (1948) classic study showing that predation can introduce variation in competitive ability, notes that "considerable ambiguity and misunderstanding has resulted from defining the competition process solely according to its consequences." He further notes that this ambiguity

has obscured the more important fact "that the selective elimination of species . . . requires an extremely long time" and that "coexistence even in crowded populations seems to require such a slight alteration in a single factor," such as temperature or predation in Park's experiments.

Quite independent of one's choice of definitions, the question remains: What are the ultimate causes selecting for the proximate pattern of competitive intransitivity? Local marine environments typically communicate with one another by swimming larvae. The larvae arriving at any given local environment vary considerably in space and time (Sutherland 1974, 1976, 1977, 1978; Jackson 1977b; Osman 1977; Underwood et al. 1983). Further variation arises in the relative positions of recruits settling on a local substratum. Variation in the relative position of colonies established at settlement results in asymmetrical encounters between colonies (that is, at different sizes, densities, angles, and so forth). Intra- and interspecific competitive ability is known to vary as a function of these encounter asymmetries (size: Connell 1961a, Day 1977, Buss 1980, Russ 1982; encounter angle: Jackson 1979b, Buss 1981b, Rubin 1982; density: Buss 1981a), suggesting that competitive ability may be adapted to exploit particular classes of settlement-induced encounter asymmetries. Competitive intransitivity, thus, may ultimately reflect adaptations of organisms to variation in the timing and location of settlement, such that the various proximate patterns in competitive rankings and community organization result from the interaction of particular settlement patterns with postsettlement processes such as predation.

ACKNOWLEDGMENTS

I thank K. Carle, J. Lubchenco, J. Moore, R. T. Paine, J. Roughgarden, R. S. Steneck, D. Wetthey, S. Woodin, P. Yodzis, and P. Yund for discussion or comments on the manuscript and the National Science Foundation (Grant OCE 81-61795) for support.